PROTEROCHAMPSA BARRIONUEVOI AND THE EARLY EVOLUTION OF THE CROCODILIA

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INTRODUCTION

During the months April through June of 1958 a joint expedition of the Museo Argentino de Ciencias Naturales and the Museum of Comparative Zoology explored continental deposits in the Province of Mendoza and San Juan in western Argentina. The last six weeks of the field season were spent in Triassic beds at Ischigualasto, a valley in the northeastern part of the province of San Juan. Fossils at this locality proved to be so abundant and so easily found that Romer (1962) has described it as a "paleontologist's dream." The crocodilians described in this paper were found there by Professor Bryan Patterson in the upper third of the Ischigualasto Formation, approximately 160 feet from the base. The formation consists of interbedded clays, shales, and some sandstone, characterized by the variegated green, white, brown, and red colors typical of so many fossil bearing continental deposits. As regards age, Frenguelli (1948) considered the formation to be upper Keuper; Romer (1960, 1962) states that it is certainly pre-Norian and probably pre-Carnian. Gomphodont cynodonts and rhynchosaurs were found in abundance in the formation in the same general area as the material here discussed.

The following year the Instituto Miguel Lillo of the Universidad de Tucumán sent two expeditions to the area. Under the direction of Dr. Osvaldo A. Reig a number of specimens were found, some of which have already been described (Reig, 1959; Casamiquela, 1960; Bonaparte, 1962, 1963). Reig (1959) published a preliminary account of the ancestral crocodilian discussed here, giving it the name *Proterochampsa barrionuevoi.*

The material discussed in this paper consists of one complete, well preserved skull (but with parts of the ventral area badly fractured), together with 13 articulated vertebrae and ribs, MCZ 3408, and one partial skull, MACN 18165 (Museo Argentino de Ciencias Naturales).

I am obliged to Arnold D. Lewis for preparation of the material, to Dr. Bernhard Kummel for the photography, to Dr. Edwin Colbert and The American Museum of Natural History for permission to examine *Protosuchus*, to Yale Peabody Museum for making available various mesosuchians for comparative study, and to Dr. K. A. Kermack of University College London for allowing me to examine the primitive crocodilian from Wales. The manuscript has been read by Professors Bryan Patterson, Ernest Williams, and Alfred Romer. To all of these people I express my sincere thanks. The expedition was supported in part by the National Science Foundation, and in part by Life Magazine.

MORPHOLOGY

THE SKULL

General remarks: The skull of *Proterochampsa* presents a remarkable combina-

tion of primitive thecodont, advanced crocodilian, and transitional characters. The dorsal surface resembles that of a modern crocodile in the highly sculptured surface, large dorsally placed orbits, small supratemporal fenestrae, and external nares near the midline of the snout. The skull is flat, relatively broad, and has a long snout. The sculpturing of the cranial table is noteworthy in that the rugose ridges usually follow a pattern, differing in this respect from the random pitted type of sculpturing found in later crocodiles. Most of the transitional characters are in the palatal region. The presence of relatively large antorbital fenestrae and of long curved teeth may be considered transitional or primitive. Sutures on the dorsal side of the skull are generally well preserved; on the underside, however, it is much more difficult to determine the bone pattern due to the fractured nature of the region.

The occipital face of the skull of *Proterochampsa* resembles that of a somewhat flattened version of a modern crocodile. Although the skull is 35 centimeters from the occipital condyle to the tip of the snout, it is only 4 centimeters high from the base of the occipital condyle to the top of the parietal. Of course, some allowance must be made for flattening and deformation in the process of fossilization, but the general aspect of length to depth remains the same (a modern crocodile of comparable size measured only 6 centimeters in depth from condyle to parietal).

The ventral portion of the skull is by no means as well preserved as the dorsal; fortunately, however, the position of the internal nares and the limits of the secondary palate are quite clear. The basisphenoid, the pterygoid flange and its tooth row, and the ectopterygoid relationships are clearly seen. The rest of the basicranial region is crushed and distorted. The interpretation presented here necessarily contains an element of the speculative.

Premaxilla. The premaxilla occupies the anterior end of the snout extending back from the "canine notch" toward the midline, forming an inverted V-shaped suture with the nasal and the maxilla. Ventrally, the premaxilla folds over and joins at the midline to form the anterior part of the secondary palate. The ventral suture of the maxilla and premaxilla is not visible, nor is it possible to verify the presence of an incisive foramen. The premaxilla bears six teeth. The shape and sutural relations of the dorsal side of this bone are very similar to those of a modern crocodile (see Plate V).

Maxilla. The maxilla extends posteriorly and laterally from the "canine notch," forms the anterior border of the antorbital fenestra, and joins the nasal medially and the jugal posteriorly. The maxilla in MCZ 3408 bears eleven teeth, and that of MACN 18165 at least twelve. Like the premaxilla, the sutural configuration of the maxilla is very much like that of modern crocodiles (see Plate V). Ventrally, the maxilla folds over to join with the premaxilla in the formation of the secondary palate. In this region there is no definite border delimiting the maxilla with relation to the internal nares and the palatine bones. There is, however, a slight difference in the color of the bone, which is symmetrical on both sides of the midline and has been taken as the probable boundary of the maxilla with the palatine. The maxillae are comparatively small ventrally, extending down from the posterolateral side of the upper jaw, meeting at the midline with the premaxillae, with a small process entering into the anterior border of the internal nares.

Nasal. The nasal bone of *Proterochampsa* forms a horizontal plate extending from an inverted V-shaped posterior border with the frontal and prefrontal to an anterior V-shaped suture with the premaxilla. A prominent, sculptured ridge runs longitudinally down the medial side of each nasal. Ventrally, the relationships are obscure, although it appears that there is a contact of the vomer with the nasal anterior to the internal naris. The nasal extends somewhat

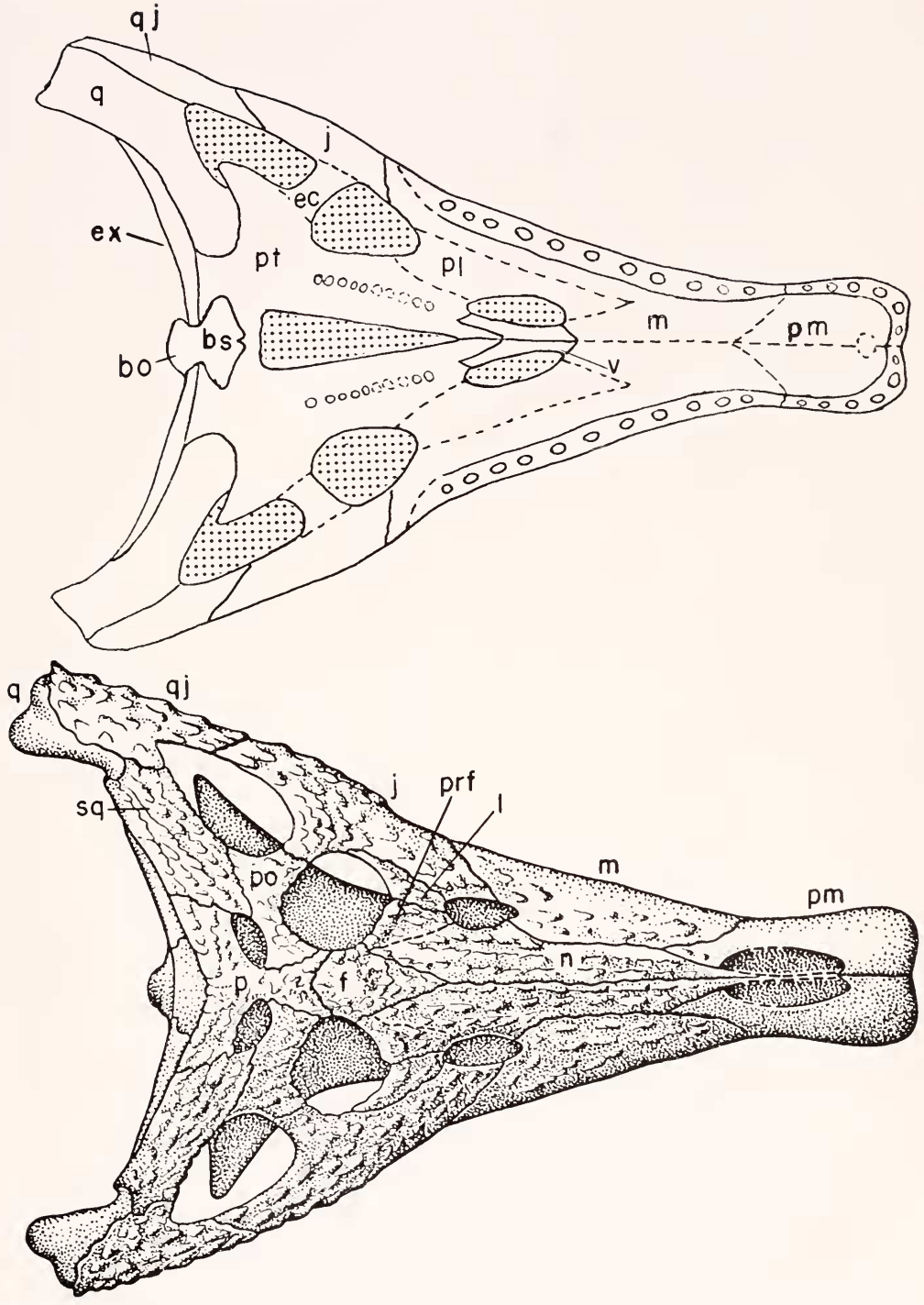


Fig. 1. Dorsal and ventral views of skull of *Proterochampsa barrionuevoi*, MCZ 3408. × 1/3. Abbreviations on page 436.

laterally at the antorbital fenestra, of which it forms the medial border.

Prefrontal. The suture of the prefrontal with the nasal is not clearly visible; it is inferred from the change in pattern of the bone and the orientation of the sculpturing in this area. The prefrontal stands out as a highly sculptured triangular bone forming the anteromedial border of the orbit and the posteromedial border of the antorbital fenestra. At the border with the lacrimal, the prefrontal is also marked by the strong sculptured crest extending around all but the lateral one-third of the orbit (see discussion of orbit below). The prefrontal is bordered medially by the nasal, anteriorly by the antorbital fenestra, laterally by the lacrimal, and posteriorly by the orbit and a small part of the frontal.

Lacrimal. The lacrimal of *Protorochampsa* is smaller than in later crocodiles. It is a triangular, lightly sculptured bone bordered by the jugal laterally, the prefrontal medially, the antorbital fenestra anteriorly, and the orbit posteriorly. It is distinctive in not having an orbital crest along its border with the orbit. The lacrimal inclines somewhat laterally; it is primitive in that it extends around a large part of the lateral margin of the orbit, but advanced as regards small size.

Frontal. The frontals are fused at the midline but there is still an indication of a suture between them. The sculpture pattern of the frontals is distinctive in consisting of transverse ridges forming peaks at the midline, slanting laterally, then sweeping up at the margin of the orbit to join in the orbital crest. The conjoined frontals have a triangular shape and look rather like an arrowhead pointing down the snout. They are bordered anteriorly by the nasals and the prefrontals, posteriorly by the parietals, and laterally by the orbits.

Parietal. The parietals are completely fused, with no trace at all of a suture separating them. They are slightly concave at the midline anterior to the supratemporal fenestrae, and slope upward posteriorly to form part of the occipital crest. Small ridges, not as prominent as those of the frontals, radiate out from the center of the fused parietals, becoming quite prominent posteriorly near the occipital crest. The parietals are roughly T-shaped, with the crossbar of the T forming part of the occipital crest. They are bordered posterolaterally by the squamosals, posteriorly by the supraoccipital and the exoccipitals, laterally by the postorbitals and anteriorly by the frontals. A very small lateral part enters the orbit, and the entire posterior border of the supratemporal fenestra is formed by the anterior edge of the crossbar portion of the bone.

Postorbital. The postorbital is a massive, heavily sculptured bone forming the greater part of the posterior margin of the orbit. It is bordered medially by the parietal, posteriorly by the squamosal, and laterally by the jugal. The postorbital participates in the formation of the orbit anteriorly, the supratemporal fenestra posteromedially, and forms the medial edge of the infratemporal fenestra laterally. Together with a medial extension of the jugal it forms the postorbital bar. Although the form of the bar is very similar to that of modern crocodiles, it remains entirely on the dorsal surface of the skull.

Squamosal. The squamosal forms the principal part of the occipital crest. It is a strong, massive bone with highly sculptured, very prominent ridges extending laterally along the occipital crest. Other ridges extend diagonally from the postorbital in front of the supratemporal fenestra and back across the squamosal to the lateral edge of the cranial table. Reig called special attention to this diagonal ridge; on the cast of the type specimen, which he kindly sent to the Museum of Comparative Zoology, this crest is much more prominent than on the specimens here described. The squamosal rests posteriorly on top of the exoccipital; laterally it meets the quadratojugal nearly horizontally, with strong sculpturing present on both bones. A small proc-

ess of the squamosal extends down the lateral border of the exoccipital. Posterolaterally the quadrate sweeps up to form a steep, smooth suture directly underneath the squamosal. The squamosal forms a small part of the lateral border of the supratemporal fenestra and the largest part of the posterior border of the infratemporal fenestra. It is bordered by the parietal, exoccipital, quadrate, quadratojugal, and postorbital.

Jugal. The position of the jugal is quite different from that of the mesosuchians and eusuchians and much more like that of some of the early thecodonts. Unlike crocodiles in general, the jugal of *Proterochampsa* forms only a minor part of the orbit, being ventral to the lacrimal for most of the orbital area. The jugal extends forward from its border with the quadratojugal to form most of the lateral border of the infratemporal fenestra; it sends a process halfway up between the orbit and the infratemporal fenestra to meet the postorbital and to form the postorbital bar, which, as just described, is not displaced downward from the cranial surface (see Fig. 2). The jugal forms a small part of the lateral border of the orbit, meets the lacrimal and continues lateral to and beyond it to form the lateral border of the antorbital fenestra. The jugal is in general more lightly sculptured than most of the dorsal skull bones. Together with the lacrimal, it forms that part of the orbit which does not have a prominent raised crest. The part that forms the bar below the infratemporal fenestra is, however, quite massive and highly sculptured.

On the palate the sutures of the jugal are not fully discernible. However, the ectopterygoid can be seen extending from the jugal, and the suture with the quadratojugal can be seen. The border with the maxilla and the exact location of the suture with the ectopterygoid are not visible.

Quadratojugal. Like the jugal, the quadratojugal resembles that of its thecodont ancestors much more closely than it does

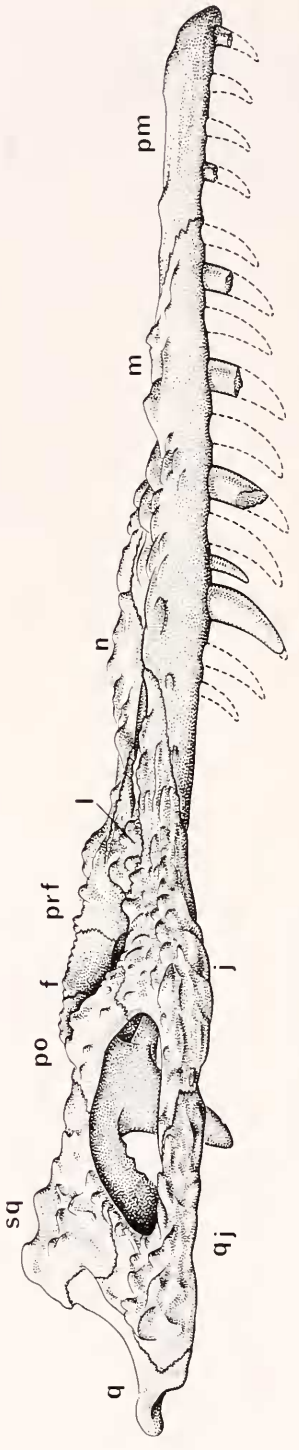


Fig. 2. Profile of *Proterochampsa barrionuevoi*, MCZ 3408. × 1/3.

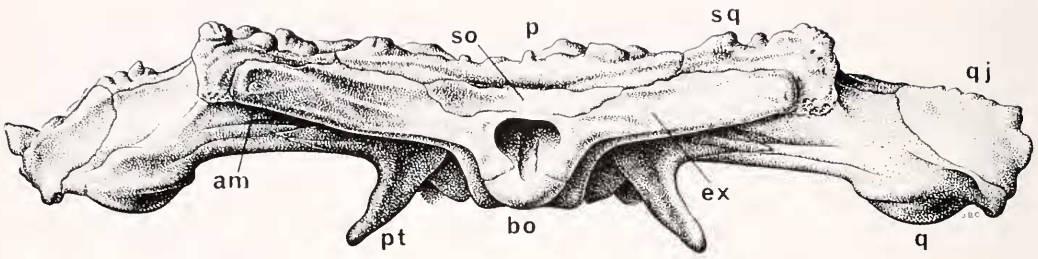


Fig. 3. Occipitol view of *Proterochampsa barrionuevoi*, MCZ 3408. × ½.

that of later crocodiles. It is much larger than the modern crocodilian quadratojugal and forms the posterolateral corner of the dorsal surface of the skull. Anteriorly, it joins with the jugal, forms the posterolateral margin of the infratemporal fossa, and unites medially with the squamosal. Posteriorly and medially, the quadratojugal has a smooth face which joins with the quadrate.

On the palatal surface, the suture of the quadratojugal and the jugal runs diagonally forward. Its other ventral contact is with the quadrate, on which it sits like a cap with the lateral edge folded under. The dorsal and lateral parts of the bone are sculptured to about the same extent as the jugal, being more massive along the infratemporal bar. The posterior face of the bone is smooth and quite steeply inclined down to its junction with the quadrate.

Quadrate. In its posterior aspect the quadrate of *Proterochampsa* resembles that of advanced crocodilians in extending upward and medially with a smooth sloping face to join the exoccipital and the squamosal; it is not, however, overlain by the latter as in eusuchians. Further, it is quite unlike Recent crocodiles in having the external auditory meatus in the form of a groove going into the inner ear along the posterodorsal part of the quadrate, anterior to the exoccipital and underneath, but not enclosed by, the squamosal (see discussion of ear region below). The configuration of the articulating condyles of the quadrate is similar to that of some of the mesosuchian crocodiles [Teleosauridae, Libycosuchidae, and Metriorhynchidae (Kälin, 1955)] in the presence of two condyles, the medial larger than the lateral. This is in contrast, on the one hand, to the usual thecodont condition of only one condyle and, on the other, to the Recent crocodilians, which have two condyles but the lateral larger than the medial.

Ventrally, the posterior edge of the quadrate forms a vertical ridge running diagonally from the articulating surface medially to join the posterior border of the pterygoid. The lateral border, covered dorsally by the quadratojugal, remains horizontal and gives rise to the vertical ridge previously mentioned. In size, the quadrate is more like that of the thecodonts than of the crocodilians, but in shape it is transitional between the two.

Supraoccipital. The supraoccipital in *Proterochampsa* is a subtriangular, smooth bone lying vertically on the posterior face of the skull, just under the fused parietals, much as in the modern crocodiles. It is bordered dorsally by the parietals, laterally by the exoccipitals, and ventrally, just above the foramen magnum, by a thin expression of the exoccipital.

Exoccipital. The exoccipital forms all but the most ventral portion of the border of the foramen magnum; it extends outward to underlie the lateral part of the parietal and the posterior part of the squamosal. The small occipital process of the squamosal forms the lateral border of the exoccipital. Laterally and ventrally the exoccipital

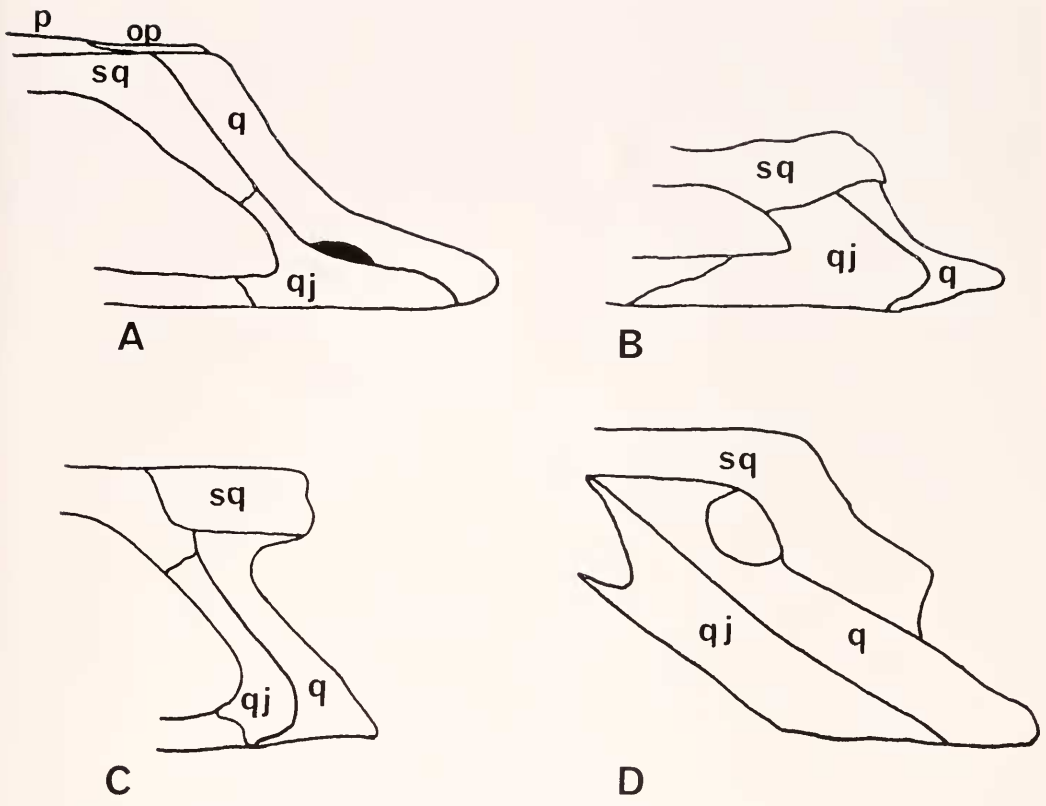


Fig. 4. External ear structure in A, *Chasmatosaurus* (proterosuchian thecadont); B, *Proterochampsa*; C, *Pelagosaurus* (mesosuchian crocadile); and D, *Crocodylus*.

joins with the quadrate. Ventrally, on the posterior face of the skull, it joins with the basioccipital.

Basioccipital. The basioccipital forms the entire occipital condyle and the most ventral border of the foramen magnum. Ventrally, it is fused completely with the basisphenoid, has a subrounded shape, resembling the thecodont rather than the eusuchian condition and is without the basioccipital processes common in mesosuchians.

Ear structure. Proterochampsa shows the beginning of the acquisition of the otic notch in crocodiles, and, with the mesosuchians, provides a phylogenetic sequence for the evolution of the unusual crocodilian ear structure (Fig. 4). In *Proterochampsa* there is a meatal groove running from the border of the quadrate and squamosal, passing anterior to the exoccipital and into the inner ear. Haughton (1924) mentions a similar groove in *Notochampsa*. In *Protosuchus* there is no evidence of either a groove or an otic notch.

In the earliest thecodonts, there is no indication of an otic notch (later thecodonts do possess one, although it is usually formed completely within the squamosal), and the quadrate is, as a rule, completely vertical.

In mesosuchians the otic notch is usually quite prominent, formed by the squamosal projecting out over the quadrate (see Fig. 4C). In modern crocodiles the squamosal has extended backward and downward onto the quadrate to close the otic notch and gain a broad posterior contact with the

Fig. 5. Comparison of the external auditory meatus in *Crocodylus* (*left*) (X-ray, after Edinger, 1938), and *Proterochampsa* (*right*).

quadrate, forming, with the exoccipital, the deep pocket of the external and middle ear structures. This closing of the otic notch has been accompanied by a displacement of the tympanic cavity laterally from the braincase. This is already shown by some late Cretaceous mesosuchians of the family Notosuchidae (Kälin, 1955), in which the quadrate has become more posteriorly inclined (and the skull much more flattened). In this respect the quadrate of *Proterochampsa* resembles that of mesosuchians in both inclination and height.

Although the acquisition of the otic notch appears to follow the developmental sequence outlined above, it should be emphasized that this sequence is based more on external form than on a detailed comparative study of the osteology of the ear region of fossil crocodilians.

Dorsal openings of the skull. The external nares lie on either side of the midline, separated at least in part (and probably entirely) by the slender tip of the paired nasals. They are approximately five centimeters long, two and a half centimeters across, and oval shaped. They are completely enclosed by the premaxillae, except for the nasal process which separates them.

The antorbital fenestrae are oval-shaped openings, somewhat wider posteriorly than anteriorly. Like the external nares, they are completely dorsal. They are bordered by the maxilla, nasal, prefrontal, lacrimal, and jugal (as previously described).

The orbits of *Proterochampsa* are quite like those of modern crocodiles in being almost completely within the horizontal plane of the skull (there is a small lateral angle downward as in modern crocodiles). However, as in thecodonts and early crocodilians, the postorbital bar is still at the dorsal surface of the skull and the lacrimal bone plays an important part in the border of the orbit. The orbit is bordered by a very strong crest that extends around all but the anterolateral one-third of the circumference. Anteriorly, the crest stops at the lateral edge of the prefrontal part of the border to run down the prefrontal to the antorbital fenestra. Posteriorly, the encircling crest stops at the edge of the postorbital, halfway down the postorbital bar, and another crest goes off diagonally at the beginning of the postorbital bar across the postorbital and squamosal bones.

The supratemporal openings are considerably smaller than the infratemporal open-

ings, as is the case in Recent Crocodilia. This condition is probably primitive and, as indicated by Colbert and Mook (1951), was lost in the mesosuchians and reacquired in the eusuchians. In *Proterochampsa* these openings are nearly horizontal, slanting slightly downward towards the orbits from the prominent crests of the parietal.

The infratemporal openings of *Proterochampsa* are much larger than those of Recent crocodiles, being about as large relative to the orbits as in thecodonts. In the latter, however, they are vertical, whereas in *Proterochampsa* they lie at about a 45° angle.

Secondary palate. The secondary palate of *Proterochampsa* is of great interest. As mentioned above, it consists of the premaxillae, the maxillae, and possibly a small part of the palatines. The premaxillae and the maxillae simply extend over to the midline, and the internal nares open at the posterior border of the maxillae. They are bordered laterally by the palatines and separated by the vomers. This arrangement provides an almost perfect transition between the thecodont type of palate and the mesosuchian, in which the internal nares have moved back to the posterior border of the palatines.

Palatine. The palatine bones cannot be clearly distinguished in the two skulls available for study. However, on the basis of a slight color and textural difference of the bone which follows the general osteological pattern of crocodiles and is symmetrical on both sides of the midline, the medial boundaries are tentatively placed at the lateral borders of the internal nares. If this is correct, the palatines, in addition to bordering the internal nares, form part of the anterolateral margins of the pterygoid fenestrae.

Vomer. The vomers diverge from the midline between the internal nares, emerge on the dorsal side of the secondary palate and extend posteriorly and laterally to reveal a V-shaped exposure of the pterygoids above and between them (Plate VII). The vomers form the medial border of the internal nares.

Pterygoid. The pterygoids are the largest of the basicranial elements, consisting of an anterior plate, a flange, and a posterior process from the base of the flange. In the available specimens the anterior part of the pterygoid is badly fractured, but a row of eight to twelve very small teeth is nevertheless visible extending from just behind the internal nares to the base of the pterygoid flange. At the midline the pterygoids are separated by an interpterygoid fenestra situated between the internal nares and the basisphenoid. Here the pterygoid border is formed by a prominent ridge extending from the vomer to the pterygoid flange. Laterally, the ectopterygoid joins the pterygoid at the anterior margin of the pterygoid flange. This flange in *Proterochampsa* is similar to that of modern Crocodilia in its flat, blade-like shape. It differs from that of Recent crocodiles in not being appreciably extended downward beyond the level of the jugal. The posterior edge of the flange curves medially and dorsally to meet the medial process of the quadrate.

Ectopterygoid. The ectopterygoid forms a bar between the pterygoid fenestra and the open area around the pterygoid flange (it is well preserved and is a simple straightforward bone). It is relatively short and is bordered medially by the pterygoid and laterally by the jugal.

Basisphenoid. The basisphenoid bears no resemblance at all to that of modern crocodiles. It is small, sub-rounded and completely fused with the basioccipital. On its anterior face are two flangelike processes with a median cleft between them (which may be the eustachian tube). Just behind these processes are two prominent openings assumed to be the carotid foramina. The area immediately around the basisphenoid is badly fractured, making its relationship with the pterygoid somewhat obscure. It appears, however, to be in con-

tact with the posterior border of the pterygoid, slightly ventral to it.

Ventral openings of the skull. It is not possible to determine the size of the incisive foramen due to the mandible being pushed up into the skull and obscuring the anterior portion of the palate.

The internal nares are approximately five centimeters long by one and a half centimeters wide and extend slightly lateral from the midline, being bordered as previously described.

The interpterygoid fenestra is a triangular-shaped opening separating the pterygoids at the midline. It is seven centimeters long by three centimeters wide at its base.

The pterygoid fenestrae are oval-shaped openings. They are formed on the lateral side of the pterygoid and are approximately five and a half centimeters long by two centimeters wide. They are inclined slightly toward the midline and are narrower anteriorly than posteriorly.

MANDIBLE

The mandible is present in MCZ 3408, but is crushed up into the skull, leaving only the ventral surface visible. Although it is not possible to give a complete description of the jaw, there are some interesting features to be noted. The anterior part of the mandible is quite like that of *Crocodylus*, with a relatively narrow, oval-shaped ramus, the symphysis extending to about the fourth tooth, and not including the splenial. Posterior to the dentary, however, the mandible flares out to a broad articular surface at only a slight angle, with what is presumed to be the prearticular becoming quite thin laterally. The articular is, so far as can be determined, much larger than in other crocodiles or in thecodonts, forming the entire ventral surface of the articular region. A distinctive feature is the complete lack of a retroarticular process. The angular is relatively small, lying ventral to the articular and not extending beyond the maximum curvature of the angle. The adductor fossa is quite shallow and elongate, the floor apparently formed largely by the articular. A small elongate external fenestra is present; the articular participates in its posterior border.

This would appear to be a rather weak jaw for an aggressive carnivore, and, taking into account the relatively small number of teeth (17 total, with a third of these probably undergoing replacement at any one time), the mandible may be considered primitive or may indicate a specialized diet, perhaps fish or carrion.

DENTITION

There is a slight amount of dental differentiation in *Proterochampsa* as shown by the smaller alveoli at the anterior end of the snout. A slight constriction is present across the snout in the region of the premaxilla, which may have served to accommodate larger teeth in the lower jaw, but this is not a canine notch in the usual sense of the word. The maxillary tooth row is distinctive in extending back only as far as the anterior border of the orbit and containing only 11 teeth. About one-third of these appear to have been undergoing replacement, giving the animal only 8 or 9 operating maxillary teeth. The teeth are relatively long, slightly curved posteriorly, and slightly ovoid, the largest ones lying in the center of the maxilla, resembling those of the early mesosuchians. The mandibular teeth were not visible in either of the specimens examined.

The palatal teeth of *Proterochampsa* are extremely small, the largest being about two millimeters in diameter. They form a row along the length of the pterygoid, each row possessing from eight to twelve teeth. It is difficult to imagine these teeth functioning as either grasping or chewing mechanisms; they were probably vestigial. The palatal teeth do, however, provide a possible link to the primitive proterosuchid thecodonts.

VERTEBRAE AND RIBS

The posteranial material consists of 13

articulated vertebrae, and most of the associated ribs of MCZ 3408, which were found in series and in articulation with the skull. All except the first bear ribs.

Cervical vertebrae. There are seven or eight cervical vertebrae preserved in *Proterochampsa.* Except for the loss of the upper part of some of the neural spines, all are well preserved.

The atlas-axis complex is similar to that of crocodiles in general; the proatlas, if present, was not preserved. The atlas consists of the two sides of the neural arch surrounding what appears to be the odontoid process. The axis resembles the other cervical vertebrae, differing only in having a wider ventral keel, small, diagonally placed parapophyses and the characteristically larger neural spine. The rib of the axis is a normal rib, differing from the other cervical ribs only in articulating more anteriorly on the centrum. This is in contrast to the highly modified splint-like rib of the axis of modern crocodiles.

The remaining cervical vertebrae are rather lightly constructed with quite thin and comparatively long neural spines. The centra are strongly amphicoelous, slightly longer than high, oval in cross section but with prominent ventral keels. The neural arch lies relatively low on the centrum, with the diapophyses extending straight down the sides to just below the neurocentral suture. The diapophysis appears to angle slightly posteriorly in the more posterior cervicals. The base of the diapophysis is very strong, extending like an inverted triangle the entire length of each of the neural arches. The parapophysis is a small, flattened, oval-shaped process projecting outward from the base of the centrum just below, and slightly anterior to the diapophysis; that of the last two cervicals projects somewhat posteriorly. Unlike modern crocodiles, the capitular facets face straight outward instead of downward.

The anterior zygapophysis projects forward from the sub-triangular body of the neural arch as a blade-like process, with the articular surface facing dorsally and medially. In all of the cervicals it overhangs considerably the anterior edge of the centrum.

The posterior zygapophysis extends to the midline above the centrum (see Plate IX). It does not overhang the posterior face of the centrum. The articular facet lies just under the neural spine, facing downward and slightly outward. The articular surface of both zygapophyses is considerably more near the horizontal than that of modern crocodiles.

The neural spine is a narrow plate about twice the height of the centrum, arising from the posterior part of the neural arch just above the posterior zygapophysis and curving slightly backward. The neural spine becomes somewhat broader in the posterior cervical vertebrae.

Anterior dorsal vertebrae. Like the cervicals the dorsal vertebrae are strongly amphicoelous, with the centrum slightly longer than high. The transverse process projects out and down from the neural arch for a distance equaling the length of the centrum, reaching to about the level of the neuro-central suture. It is a relatively wide, blade-like process similar to that of modern crocodilians. The parapophysis, situated anteriorly and ventrally on the side of the centrum is very short and faces straight out, thus differing considerably from the more advanced crocodilian condition in which both heads of the rib articulate on the transverse process. The dorsal centra resemble those of the cervicals in being strongly keeled, but are more heavily constructed. The anterior zygapophysis is similar in general to that of the cervical vertebrae, although somewhat shorter and sturdier. The posterior zygapophysis is also very similar to that of the cervical, but somewhat stronger and has a more prominent median cleft. The neural spines of the dorsal vertebrae are wider and heavier than in the cervicals, and arise from the posterior edge of the neural arch.

Ribs. All the ribs preserved are bicipital

and articulate dorsally and ventrally (not on the same level, as do those of modern crocodiles). The cervical ribs are well developed, differing only slightly from those of eusuchians. The first cervical rib is a slender, two-headed element attached to the normal diapophysis and to a very small parapophysis, which is nothing more than an articular facet facing laterally and anteriorly on the bottom of the centrum near the anterior edge. The remaining cervical ribs are relatively slender and project posteriorly. They become longer and sturdier posteriorly and thus grade into the size of the dorsal ribs. The articulation of the tuberculum with the diapophysis on the transverse process is considerably larger than in later crocodiles, occupying the entire face of the process. The capitulum articulates ventrally and slightly anteriorly to the tuberculum. These ribs possess what appear to be the beginnings of uncinate "bulges," located about one-third of the way down the rib body and bearing prominent ridges on the anterior edges of their dorsal surfaces.

DISCUSSION

HISTORICAL REVIEW

The affinities of primitive crocodilians are uncertain due to the small number of early forms so far known. In addition to the Middle Triassic *Proterochampsa*, these are: *Protosuchus* of North America, and *Notochampsa* and *Erythrochampsa* of South Africa. (A questionable crocodilian two centimeters long, without skull or limbs, was described by Young in 1951 from the Upper Triassic of China; also an undescribed crocodilian from the Upper Triassic of Wales has been reported by Kermack [1956].) Of these three, *Protosuchus* is known from a skeleton, the other two from much less complete material. All three are late Triassic or earliest Jurassic in age.

Notochampsa istedana was described by Broom (1904) from the impressions of the undersides of most of the roofing bones of a skull, most of the dorsal armor, a scapula, a coracoid, parts of a humerus, radius and ulna, part of a femur, and parts of a tibia and fibula. A second specimen from the same general area (Barkly East, Cape Province, South Africa) was named by him *Notochampsa longipes*. This specimen consisted of a well preserved pelvis, a femur, tibia and fibula, some foot bones, and part of the dorsal armor. Both specimens were found in the upper part of the Stormberg series. Broom placed the two species in the same genus on the basis of the similarity of the dorsal armor.

Haughton (1924) excluded *Notochampsa istedana* from the Crocodilia and grouped it with *Pedeticosaurus* in a family Notochampsidae, which he referred to the thecodont suborder Pseudosuchia. He considered the family to be intermediate between the aëtosaurian thecodonts and the crocodiles. The other species, *N. longipes*, he separated from *Notochampsa*, placing it within the Crocodilia but not in any family, giving the following reason (1924:369):

"If Broom's *N. longipes* is to be kept in the genus *Notochampsa* then the genus must be considered to be characterised by the possession of a skull differing from that of a true Crocodile and of a typically crocodilian pelvis. This is not impossible; but until more is known of these forms it would seem best to separate the two forms from one another, classing *istedana* as one of the higher Pseudosuchians and erecting, as above, a new genus *Erythrochampsa* for the more truly Crocodilian *Erythrochampsa longipes*." This explanation reflects the then current philosophy of graded rather than mosaic evolution and may not be justifiable.

The following year von Huene (1925) studied the material and came to the conclusion that both genera were pseudosuchian thecodonts, forming the end members of an evolutionary sequence leading towards the crocodiles from the pseudosuchians. The sequence he proposed consisted of the following forms: *Erpetosuchus*, *Actosaurus*,

Stegomosuchus, *Sphenosuchus*, *Pedeticosaurus*, *Notochampsa* and, finally, *Erythrochampsa*.

Broom returned to the subject of *Notochampsa* and *Erythrochampsa* in 1927. He reviewed the work of Haughton and of von Huene and agreed to the generic separation of *Notochampsa* and *Erythrochampsa*, but remained firm in his conviction that they are closely related and are true crocodiles. He modified the classifications of Haughton and von Huene by placing both genera in the Notochampsidae and referring the family to the order Crocodilia.

No further information regarding the ancestry of crocodiles appeared until 1933, when Brown reported the well preserved crocodilian from the Upper Triassic or Lower Jurassic rocks of Arizona, to which he gave the name *Protosuchus richardsoni*, erecting for it the family Protosuchidae. Unfortunately, as in the other early crocodiles, nothing is preserved of the palatal region of *Protosuchus*.

The following year (1934) Mook presented a classification of the Crocodilia in which the Protosuchidae was placed in a new suborder, the Protosuchia, and no mention at all was made of either *Notochampsa* or *Erythrochampsa* as members of the Crocodilia. Romer (1945) combined *Protosuchus*, *Notochampsa*, *Erythrochampsa* and, questionably, *Pedeticosaurus* in the family Notochampsidae. In 1951 Colbert and Mook published a thorough description of *Protosuchus*, and placed *Notochampsa* and *Erythrochampsa* in the suborder Protosuchia as members of the family Protosuchidae.

Kälin (1955) modified Colbert and Mook's classification by removing *Notochampsa* and *Erythrochampsa* from the Protosuchidae and reuniting them in the Notochampsidae. He recognized the suborder Protosuchia and referred the Notochampsidae to it. The current classification of ancestral crocodilians is as follows:

Protosuchia
Protosuchidae
Protosuchus
Notochampsidae
Notochampsa
Erythrochampsa

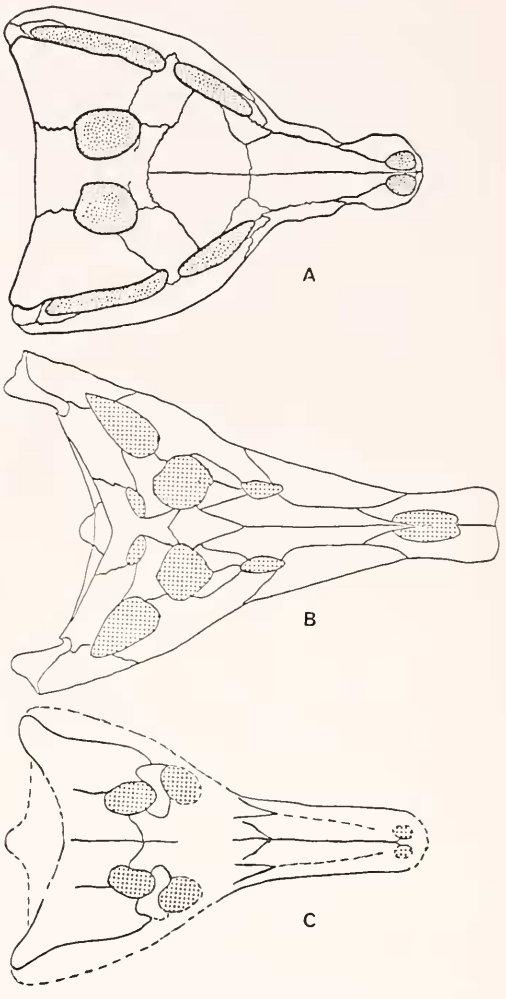


Fig. 6. Comparison of dorsal view of skull in A, *Protosuchus*; B, *Proterochampsa*; C, *Notochampsa*; not drawn to scale. (A, after Colbert and Mook; C, after Broom.)

The discovery of *Proterochampsa* requires a reappraisal.

THE AFFINITIES OF *PROTEROCHAMPSA*

In comparing *Proterochampsa* with these early crocodilians and with members of the

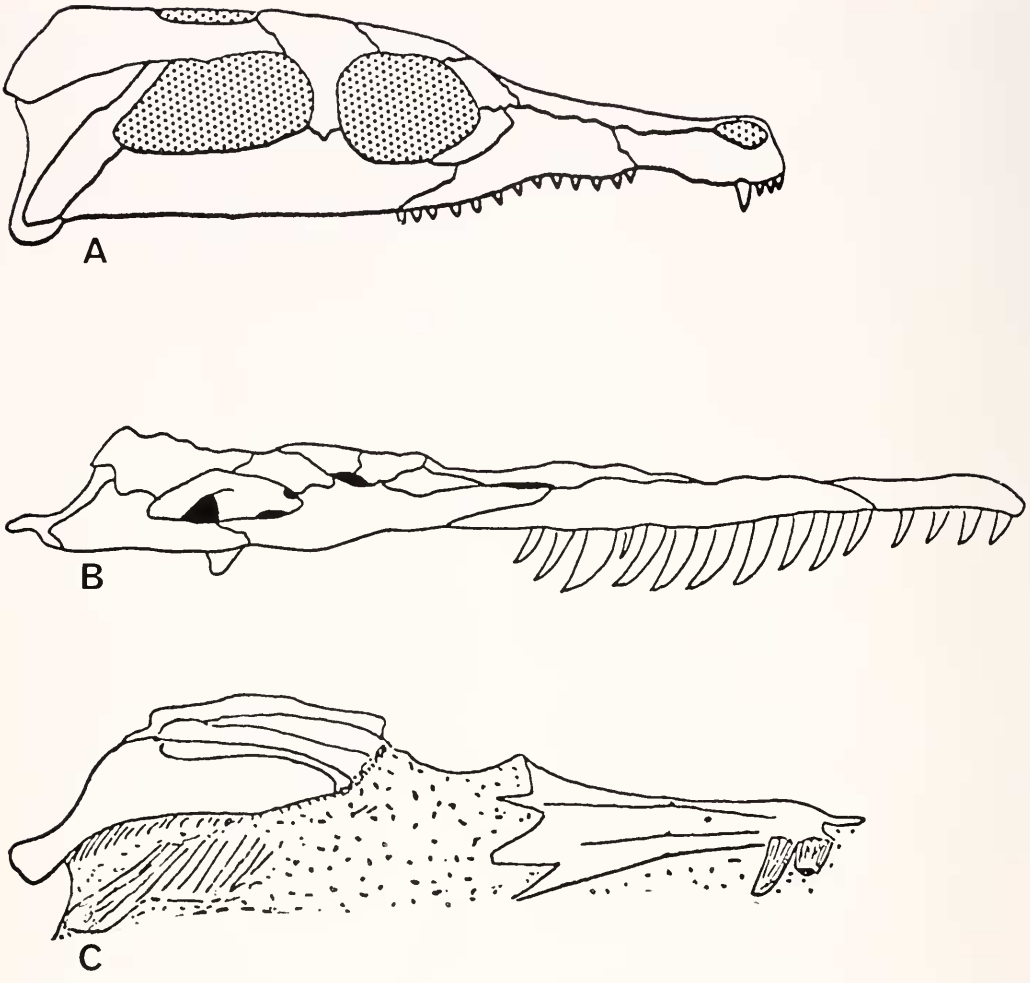


Fig. 7. Profile comparison of skulls of A, *Protosuchus*; B, *Proterochampsa*; C, *Notochampsa*; not drawn to scale. (A, after Colbert and Mook; C, after von Huene.)

Thecodontia, it becomes evident that *Proterochampsa* represents an excellent example of mosaic evolution and provides many of the characters expected in a transitional form. The snout and the dorsum of the skull generally are indistinguishable from those of a modern crocodile (except for the primitive antorbital fenestrae). On the other hand, the posterior part is remarkably like that of a primitive thecodont, except for its flatness and reduced supratemporal fenestrae. The palatal area is again quite like that of the primitive thecodonts except for the transitional features of the secondary palate and the development of the pterygoid flanges.

In trying to place *Proterochampsa* within the classification of the early Crocodilia we are faced as usual with the problems presented by inadequate material. Of *Proterochampsa* we have only the skull and a few vertebrae and ribs. *Protosuchus* is known from a skeleton, but the skull is imperfect, especially as regards the ventral surface; *Notochampsa* is represented by a very poor skull and some postcranial ma-

terial; and *Erythrochampsa* is known only from posteranial elements. The main basis for relating *Protosuchus*, *Notochampsa*, and *Erythrochampsa* to each other has been the character of the posteranium: principally the similarities of the pectoral girdles of *Notochampsa* and *Protosuchus* and the pelvic girdles of *Erythrochampsa* and *Protosuchus*.

When the skull of *Proterochampsa* is compared with that of *Protosuchus* it is immediately apparent that they do not resemble one another sufficiently to be considered as members of the same phylogenetic line. The skull of *Protosuchus* is short relative to width and considerably deeper than either *Proterochampsa* or *Notochampsa* (see Figure 10). The orbits of *Protosuchus* are nearly on a vertical plane, facing outward and forward, while those of *Proterochampsa* are on a horizontal plane, facing upward. The snout of *Protosuchus* is short (less than half the total length of the skull) and lacks antorbital fenestrae, while that of *Proterochampsa* is long (over half the total skull length), and has prominent antorbital fenestrae. *Protosuchus* has a very lightly sculptured skull compared to the heavily sculptured skull of *Proterochampsa*. In *Protosuchus* the external nares are small, clearly separated, and at the very tip of the snout. Those of *Proterochampsa* are quite the opposite, being elongate, separated only by a thin nasal process and situated considerably back from the tip of the snout. In *Protosuchus* the squamosal is large and overlies the quadrate and quadratojugal completely; in *Proterochampsa* the squamosal is relatively small and overlies none of the quadratojugal and only a part of the quadrate.

The resemblances between the two forms are not impressive. Both have sculptured skulls (although different sculpturing), small supratemporal fenestrae, amphicoelous vertebrae, and a relatively small atlas. Both *Protosuchus* and *Proterochampsa* are crocodilians, but on the basis of skull morphology it would appear that *Proterochampsa* is closer to the main line of crocodilian evolution than is *Protosuchus*.

A much closer resemblance exists between *Proterochampsa* and *Notochampsa* as regards the skull. In *Notochampsa* this is relatively long compared to width (the snout occupies more than half the length of the skull), is relatively flat, and the orbits are in the horizontal plane, all of these features being in common with *Proterochampsa*. Both *Proterochampsa* and *Notochampsa* possess an auditory canal on the posterior face of the skull. Regarding the presence of antorbital fenestrae in *Notochampsa*, Broom says there are none, von Huene says there are, and Haughton was unable to decide; the specimen is too imperfect for a definite decision.

The skulls of *Notochampsa* and *Proterochampsa* quite evidently resemble each other more than either of them resembles *Protosuchus*. This presents the problem of the taxonomic position of *Proterochampsa* and indeed requires a re-evaluation of *Protosuchus* as an ancestral crocodile and of the role of the pseudosuchian thecodonts as possible ancestors.

Proterochampsa does not belong in the suborder Protosuchia on the basis of most taxonomic characters now used to define that group. The possibilities of phylogenetic placement then are the following: the suborder Protosuchia may be redefined as a group including all pre-Jurassic crocodilians without special regard to morphological similarities, and *Proterochampsa* placed in it; or *Proterochampsa*, *Notochampsa*, and *Erythrochampsa* may be grouped into a separate suborder leading to the Mesosuchia, and the Protosuchia retained as an aberrant lineage arising from the early crocodilian stock.

On the basis of skull comparison, it appears likely that *Protosuchus* is an aberrant offshoot from the line which gave rise to the Crocodilia, possessing some characters of both thecodonts and crocodiles. It may be argued that *Proterochampsa* cannot be legitimately compared to *Protosuchus* until

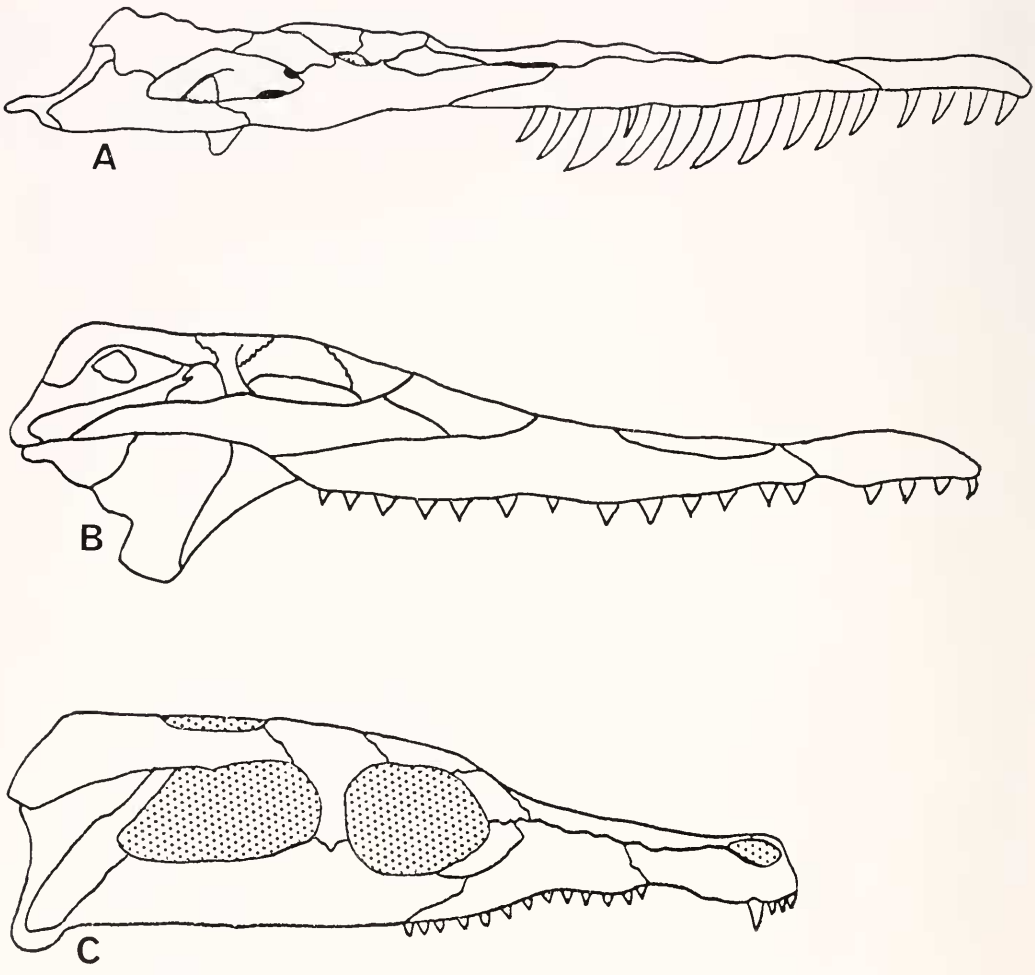


Fig. 8. Profile comparison of skulls of A, *Proterochampsa*; B, *Crocodylus*; C, *Protosuchus*; not drawn to scale.

something is known about the pectoral and pelvic girdles of the former. However, in this respect there are only three possibilities for the girdles of *Proterochampsa*: they may be the same as *Protosuchus*, more crocodilian, or less crocodilian. None of these possibilities alters the fact that *Protosuchus* has strayed considerably from the earlier line of more typical crocodilians represented by *Proterochampsa*.

If *Protosuchus* is regarded as representing an aberrant group, one not on the direct ancestral line leading to the mesosuchians, the possibility that *Proterochampsa* and *Notochampsa* actually belong within the suborder Mesosuchia must be examined.

The suborder Mesosuchia is defined as having a secondary palate formed by the premaxillae, the maxillae, and the palatines, the pubis excluded from the acetabulum, the postorbital bar at the dorsal surface of the skull, and the vertebrae amphicoelous or platycoelous. To redefine the suborder to include *Proterochampsa* and the Notochampsidae it would be necessary, so far, only to modify the definition with regard to

the secondary palate. However, to redefine the Mesosuchia in this way would be to disrupt the classification of what appears to be a natural group, or at least a fairly uniform evolutionary grade. The acquisition of the secondary palate and internal nares of the Mesosuchia marks a significant phylogenetic stage, and is remarkably consistent throughout the nine families and thirty-seven genera of the suborder. In addition to the more primitive condition of the palate (at least in *Proterochampsa*), *Notochampsa* and *Proterochampsa* also possess a more primitive condition of the external auditory meatus, while the mesosuchians are consistent in the transitional nature of this character (see discussion of the ear). In general, the Mesosuchia presents the appearance of a well established group, greatly diversified, into which *Proterochampsa* and the Notochampsidae would fit less consistently than do any of the other families within this suborder. The remaining alternative is to place *Proterochampsa* and the Notochampsidae in a separate suborder, recognizing that the Notochampsidae are very poorly known and may later prove not to be that closely related to *Proterochampsa.* However, the elongate skull and dorsal orbits, particularly the latter, indicate that *Notochampsa* had acquired the aquatic habitus of the Crocodilia.

EARLY HISTORY OF THE CROCODILIA

The evolutionary trends within the Crocodilia only become relatively well documented after the late Jurassic, although specialized marine mesosuchians are known from the early and middle parts of this period. The early and middle Jurassic were probably times of great divergence within the order, but non-marine representatives are practically unknown, due to the lack of continental sediments of these ages. The primitive Triassic members of the order, as previously mentioned, are few in number and most of them are poorly preserved. Thus, there is a gap in knowledge from the late Triassic to the late Jurassic, coupled with a dearth of material from the earlier Triassic.

Protosuchus was the first reasonably well preserved early crocodilian found. Although not closely resembling later crocodiles, it possessed a number of crocodilian characters, especially in the postcranial skeleton. The strongly crocodilian coracoid and pubis, together with the more thecodont-like skull, suggested a pattern of gradual acquisition of crocodilian characters from a pseudosuchian ancestry. *Notochampsa* and *Erythrochampsa*, then as now, were too poorly known to contribute evidence of any great value. All of these forms were of very latest Triassic age, with *Protosuchus* considered as more or less the prototype of later crocodiles. Yet by the earliest Jurassic there existed good mesosuchian representatives; the order was by then well differentiated and was undergoing rapid radiation. This would leave very little time between the rather thecodont-like *Protosuchus* and the earliest mesosuchians. Although such rapid evolution and radiation as this view would imply might not be impossible it is rather unlikely.

The discovery of *Proterochampsa* changes all this, however, by demonstrating that a number of "modern" cranial characters of the Crocodilia were already in existence by the late Middle Triassic. The conclusion that the Crocodilia became differentiated relatively early in the history of the Thecodontia rather than being an "end product" of that group seems inescapable. *Proterochampsa* is certainly a crocodile, and at present is the best known representative of the primitive members of that group. It is of course possible that it is not the ancestor of the later crocodiles, but it appears to be closer to such an ancestor, at least morphologically, than any of the other presently known early forms.

This being so, the non-crocodilian features of *Protosuchus* might be explained in one of several ways: 1) the Crocodilia arose from a non-pseudosuchian group of aquatic

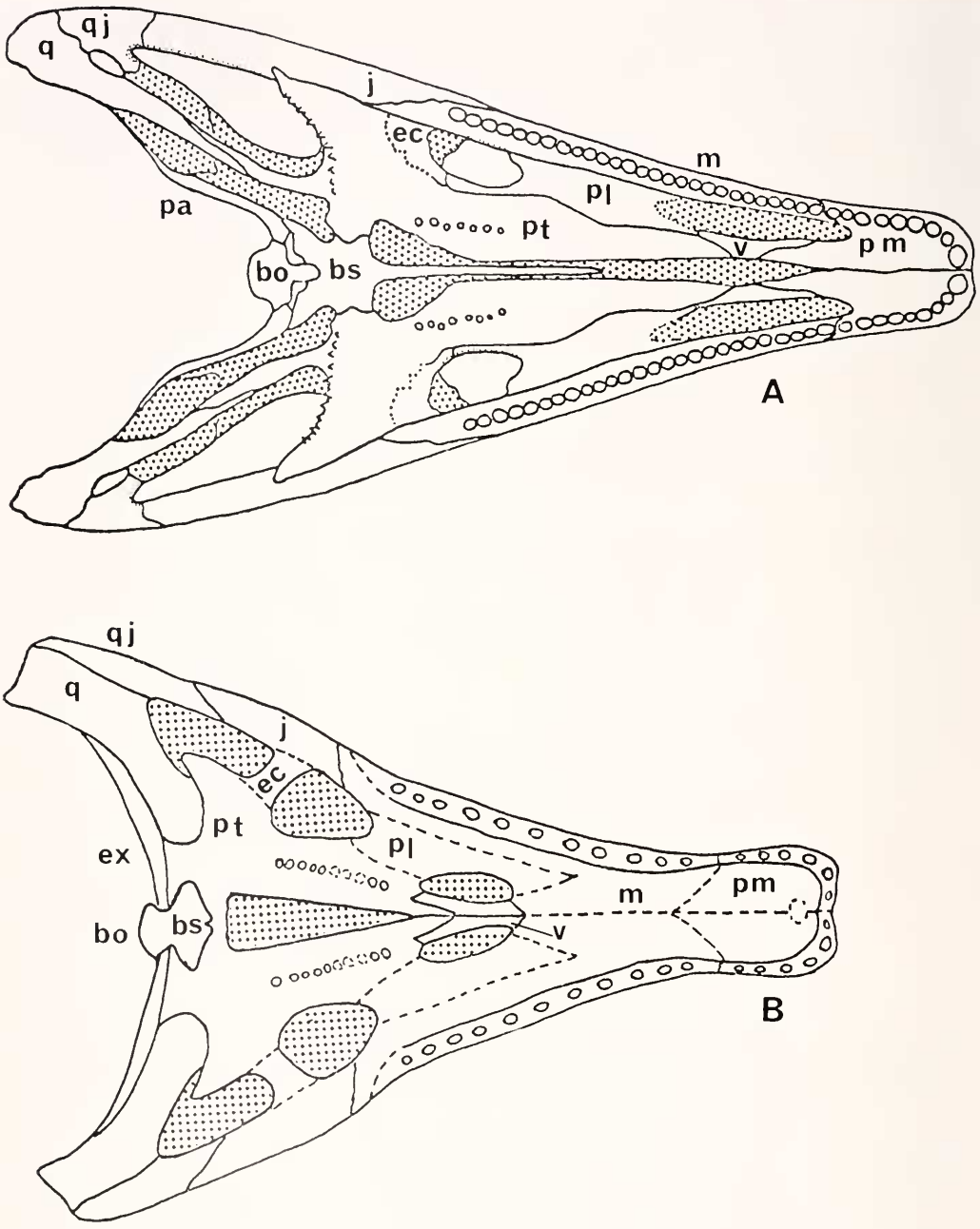


Fig. 9. Comparison of ventrol view of skull in A, *Chasmatosaurus*; and B, *Proterachampsa*. × 1/3.

thecodonts, in which case the Protosuchia could be regarded as forms that secondarily became adapted for terrestrial life; 2) the Crocodilia arose from a primitive group of terrestrial thecodonts, possibly early pseudosuchians, in which case the Protosuchia

could be regarded as having retained the primitive terrestrial features of the transitional group; 3) the Protosuchia were not true crocodilians and independently evolved crocodilian characters. Of these possibilities the last seems to be the least likely on present evidence, although the other two are almost equally uncertain. Any one of these possibilities, however, could explain the existence of groups that possessed a few good crocodilian characters but were more thecodont in habitus.

The primitive crocodilian recently discovered in the Triassic of Wales has been characterized by Dr. K. A. Kermack (pers. comm.) as a "crocodile trying to be a dinosaur." This description might be applied to some of the other archosaurs that appear to be in the "fringe area" of the Crocodilia, such as *Pedeticosaurus, Sphenosuchus, Platyognathus*, and perhaps *Hesperosuchus*. In this context *Protosuchus* might be considered as less successful in "becoming a dinosaur" than the sphenosuchians, and therefore as looking more like a typical crocodile.

The solution to the question of crocodilian origins naturally lies within the Thecodontia, but unfortunately this group is not well understood at present. Among early thecodonts, *Chasmatosaurus* somewhat resembles *Proterochampsa* in the palatal area. Although *Chasmatosaurus* is extremely primitive, it may nevertheless represent the group of thecodonts from which the Crocodilia arose.

CLASSIFICATION OF THE EARLIEST CROCODILIA

On the basis of this study it is proposed that the primitive, Triassic crocodilians be divided into two groups, the suborder Protosuchia, characterized by the Protosuchidae, and including, questionably, the sphenosuchid thecodonts, and a new suborder, the Archaeosuchia, for the Proterochampsidae and, provisionally, the Notochampsidae.

ARCHAEOSUCHIA new suborder

The Archaeosuchia may be defined as follows: Crocodilia with orbits in dorsal plane of skull, cranial table sculptured, snout long relative to width, palatines not participating in secondary palate, postorbital bar at surface of skull, auditory canal on posterior face of skull, vertebrae amphicoelous; pubis elongate, nearly or completely excluded from the acetabulum.

NOTOCHAMPSIDAE Haughton 1924

The family Notochampsidae, although erected in 1924, has never been defined. The following definition is proposed for it: premaxillae small, external nares divided, squamosals large, forming most of lateral border of cranial table, frontals not fused, participating in border of supratemporal fenestrae; coracoid enlarged, similar in shape to scapula. The type genus of the family is *Notochampsa*.

PROTEROCHAMPSIDAE new family

Proterochampsa differs from the notochampsids to a degree sufficient to warrant the erection of a family for its reception. This may be defined as follows: Archaeosuchia with external nares united at midline, premaxillae large, frontals small, fused, not participating in border of supratemporal fenestrae, squamosals small, limited to posterior border of skull. *Proterochampsa* is designated as the type genus of the family.

This would result in the following classification:

PROTOSUCHIA Mook 1934
  Protosuchidae Brown 1933
    Protosuchus Brown 1933
PROTOSUCHIA *incertae sedis*
  Sphenosuchidae Haughton 1924
    Sphenosuchus Haughton 1915
  Sphenosuchidae *incertae sedis*
    Pedeticosaurus Van Hoepen 1915
    Platyognathus Young 1944
ARCHAEOSUCHIA new suborder
  Proterochampsidae new family
    Proterochampsa Reig 1959

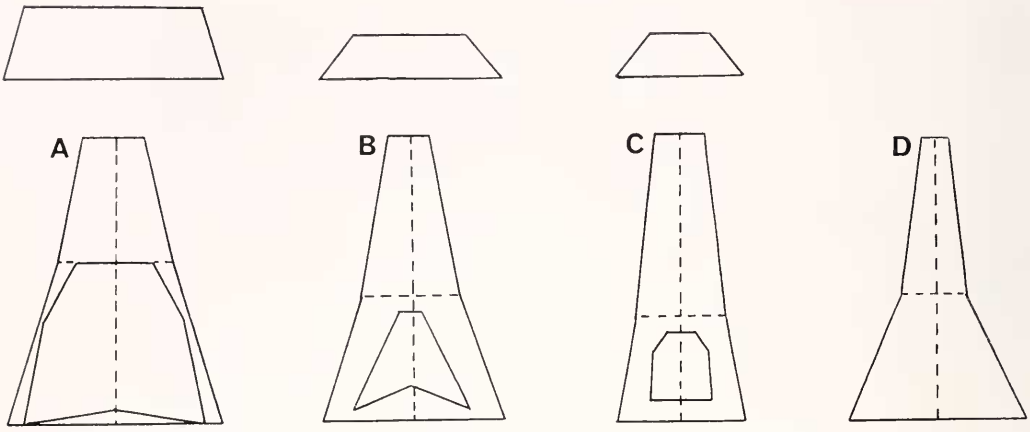


Fig. 10. Diagrammatic comparison of skull relationships of A, *Protosuchus*; B, *Proterochampsa*; C, *Crocodylus*; D, *Notochampsa*. Length of the skull is reduced to unity.

Notochampsidae Haughton 1924
Notochampsa Broom 1904
Erythrochampsa Haughton 1924

SUMMARY

Proterochampsa barrionuevoi represents a late Middle Triassic line of crocodilians showing many of the "progressive" features characteristic of later members of the order. The dorsum of the skull is almost identical with that of the modern *Crocodylus* except for the presence of an antorbital fenestra and the lateral position of the quadratojugal. Ventrally, a rudimentary secondary palate has evolved, consisting only of the premaxilla and the maxilla, while the very small pterygoid teeth and an interpterygoidal vacuity are retained. The posterior surface of the skull shows a meatal groove beginning at the ventral tip of the squamosal and passing anterior to the exoccipital. This is possibly the beginning of the reacquisition of an otic notch in the Crocodilia. The mandible is distinctive in the absence of a retroarticular process, the large size of the articular bone, and the slight angle. In general the jaw appears to have been a relatively weak structure. The marginal teeth are slightly ovoid, rather slender, and slightly curved posteriorly, fitting the typical thecodont pattern. The small number of these teeth (17) may be a primitive character or may indicate a specialized diet, perhaps fish or carrion. The pterygoid teeth are so small that it is difficult to believe they were of any great use. The skull of *Proterochampsa* shows an interesting combination of primitive, transitional, and advanced characters; it provides an excellent example of mosaic evolution.

The posteranium is represented only by the anterior vertebrae and ribs. The vertebrae are strongly amphicoeleous and have prominent keels. The ribs are all bicipital, with small uncinate processes present on those of the thoracic region.

The Crocodilia have long been considered an "end product" that arose from late Triassic thecodonts by the gradual acquisition of distinctive characters and an aquatic habitus. *Proterochampsa* provides evidence that the major features of crocodilian skull structure were in existence by the latter part of the Middle Triassic. A re-evaluation of the known primitive crocodilians suggests that there were apparently two lines of evolution during the Triassic. On one of these lines, crocodilian characters, most of which are shown in the skull of *Proterochampsa*, were evolved, while in the other, characterized by *Protosuchus*, the trend led away

from the crocodilian way of life toward a more terrestrial habitat and acquisition of the necessary morphologic features for successful competition with its thecodont relatives.

On the basis of this study the family Proterochampsidae is proposed, and the primitive crocodilians are divided into two suborders, the Protosuchia, consisting of Protosuchidae and, questionably, the sphenosuchoidean thecodonts, and a new suborder, the Archaeosuchia, for the Proterochampsidae and, provisionally, the Notochampsidae.

RESUMEN

Proterochampsa barrionuevoi representa una línea de cocodrilos del Triásico medio que muestra muchos de los rasgos "progresivos" que caracterizan a los miembros más avanzados del orden. La superficie dorsal del cráneo es casi igual a la de *Crocodylus* de la actualidad, pero retiene los carácteres primitivos de las fosas anteorbitarias y de la posición lateral del cuadrado-yugal. Por el lado ventral, muestra un paladar secundario rudimentario formado por los premaxilares y los maxilares, y a la vez retiene los pequeños dientes pterigoideos y la fosa interpterigoidea que son mas bien características de los técodontes primitivos. La superficie posterior del cráneo posee un surco meatal que comienza en el punto ventral del escamoso y pasa por delante del exoccipital. Esto puede indicar el comienzo de la adquisición de la muesca ótica en el orden Crocodilia. La mandíbula se destaca por la falta del proceso retroarticular, por el tomaño grande del articular, y por la pequeñez del angulo. En general la mandíbula parece haber sido una estructura relativamente débil. Los dientes marginales son ligeramente ovoides, delgados, y algo recurvados hacia atrás, siendo su aspecto similar al de los técodontes. El pequeño numero de estos dientes (17) puede ser un carácter primitivo o quizás un indicio de una dieta especializada, que podría haber consistido en peces o carroña. Los dientes pterigoideos son tan reducidos que resulta difícil creer que fuesen de utilidad alguna. El cráneo de *Proterochampsa* muestra una combinación sumamente interesante de carácteres primitivos, transicionales, y avanzados, por lo que proporciona un excelente ejemplo de evolución mosaico.

La región post-craneana de *Proterochampsa* está unicamente representada por las vértebras y las costillas anteriores. Las vértebras son biconcavas y tienen quillas prominentes. Las costillas son todas bicipitales y las de la región torácica poseen pequeños procesos uncinados.

Tradicionalmente se ha considerado el orden Crocodilia como el "producto final" de una cepa de técodontes del Triásico superior, diferenciándose por la adquisición gradual de carácteres típicos y un habito acuático. *Proterochampsa* demuestra que los principales rasgos diagnósticos del orden Crocodilia ya existian en el Triásico medio. Una reevaluación de los cocodrilos primitivos conocidos hasta ahora sugiere la posibilidad de que durante el Triásico habia dos líneas de evolución. En una de estas líneas se desarrollaron los rasgos típicos del orden Crocodilia, la mayor parte de los cuales se ven en el cráneo de *Proterochampsa*. La otra línea, caracterizado por *Protosuchus*, se apartó del ambiente típico de los cocodrilos hacia una vida más terrestre, con la subsiguiente adquisición de los rasgos necesarios para competir con técodontes del mismo hábito.

Como resultado de este estudio se propone la creación de la familia Proterochampsidae y la división de los cocodrilos primitivos en dos subórdenes: Protosuchia, constituida por *Protosuchus* y, presuntamente, los técodontes esfenosucoideos, y un nuevo suborden, Archaeosuchia, para la Proterochampsidae y, provisionalmente, la Notochampsidae.

LITERATURE CITED

Bonaparte, J. F. 1962. Descripción del craneo y mandibula de *Exaeretodon frenguellii*, Ca-

brera. Pub. Mus. Munic. Cienc. Nat. Trad. Mar del Plata, **1**: 135–202.

———. 1963. *Promastodonsaurus bellmani*, n. g. et n. sp., capitosaurido del Triásico Medio de Argentina. Ameghiniana, **3**: 67–77.

Broom, R. 1904. On a new crocodilian genus (*Notochampsa*) from the upper Stormberg beds of South Africa. Geol. Mag., Dec. 5, **1**: 582–584.

———. 1927. On *Pheuosuchus* and the origin of the crocodiles. Proc. Zool. Soc. London, 1927 (7): 359–370.

Brown, B. 1933. An ancestral crocodile. Amer. Mus. Novit., No. **638**: 1–4.

Casamiquela, R. M. 1960. Noticia preliminar sobre dos nuevos estagonolepoideos argentinos. Ameghiniana, **2**: 3–10.

Colbert, E. H. and C. C. Mook. 1951. The ancestral crocodilian *Protosuchus*. Bull. Amer. Mus. Nat. Hist., **97**: 149–180.

Edinger, T. 1938. Über Steinkerne von Hirn und Ohr-Höhlen der Mesosuchier *Goniopholis* und *Pholidosaurus* aus dem Buckeburger Wealden. Acta Zoologica, **19**: 467–504.

Frenguelli, J. 1948. Estratigrafía y edad del llamado Rético en la Argentina. Gaea, **8**: 159–309.

Haughton, S. H. 1915. A new thecodont from the Stormberg beds. Ann. South African Mus., **12** (3): 65–106.

———. 1924. The fauna and stratigraphy of the Stormberg series. Ann. South African Mus., **12** (8): 323–497.

Huene, F. von. 1925. Die Bedeutung der *Sphenosuchus*-Gruppe für den Ursprung der Krokodile. Zeitschr. Indukt. Abstammungs-und Vererbunglehre, **38**: 307–320.

Kälin, J. 1955. Crocodilia. *In*: Traité de Paléontologie, ed. J. Piveteau, vol. 5. Paris, Masson et Cie, pp. 695–787.

Kermack, K. A. 1956. An ancestral crocodile from South Wales. Proc. Linn. Soc. London, Session 166: 1–2.

Mook, C. C. 1934. The evolution and classification of the Crocodilia. Jour. Geol., **42**: 295–304.

Reig, O. A. 1959. Nuevos reptiles arcosaurios del Triasico de Ischigualasto. Rev. Asoc. Geol. Argentina, **13**: 257–270.

Romer, A. S. 1945. Vertebrate paleontology. Second edition. Chicago: University of Chicago Press, pp. 1–677.

———. 1960. Vertebrate-bearing continental Triassic strata in Mendoza region, Argentina. Bull. Geol. Soc. America, **71**: 1279–1294.

———. 1962. The fossiliferous Triassic deposits of Ischigualasto, Argentina. Breviora, Mus. Comp. Zool., No. **156**: 1–7.

Van Hoepen, E. C. N. 1915. Contributions to the knowledge of the reptiles of the Karroo Formation. Ann. Transvaal Mus., **5**: 83–87.

Young, C. C. 1944. On a supposed new pseudosuchian from the Upper Triassic saurischian-bearing red beds of Lufeng, Yunnan, China. Amer. Mus. Novit., No. **1264**: 1–4.

———. 1951. The Lufeng saurischian fauna in China. Paleont. Sinica, **134**: 19–95.

(*Received 4 January, 1966.*)

ABBREVIATIONS

am auditory meatus
bo basioccipital
bs basisphenoid
ec ectopterygoid
ex exoccipital
f frontal
j jugal
l lacrimal
m maxilla
n nasal
op opisthotic
p parietal
pa paraoccipital
pl palatine
pm premaxilla
po postorbital
prf prefrontal
pt pterygoid
q quadrate
qj quadratojugal
so supraoccipital
sq squamosal
v vomer

Table I

Table of Measurements in Millimeters

	MCZ 3408	MACN 18165		MCZ 3408	MACN 18165
Total length of the skull, from the posterior border of the quadrate to the end of the snout at the midline	395	440	Distance between the supratemporal fenestrae	30	—
Length of the skull from the occipital crest to the end of the snout at the midline	325	375	Distance between the orbits	41	—
Length of the skull from the occipital condyle to the end of the snout	350	—	Width of the skull between the antorbital fenestrae	58	—
Width of skull between external borders of quadratojugals	270	—	Width of the snout at the anterior border of the antorbital fenestrae	108	109
Width of skull between external borders of the orbit	130	—	Width of the snout at the "canine notch"	55	59
Maximum diameter of the orbit	45	45	Length of the snout from the anterior border of the orbit to the tip of the premaxilla	238	280
Width between the lateral borders of the supratemporal fenestrae	84	—	Length of the snout from the anterior border of the antorbital fenestra to the tip of the snout	183	208
Maximum diameter of the supratemporal fenestra	28	42	Distance from the anterior border of the internal nares to the tip of the premaxillae	—	184
Maximum diameter of the antorbital fenestra	38	44	Maximum diameter of each internal naris	—	13
Maximum diameter of the infratemporal fenestra	71	89	Distance from the posterior border of the internal nares to the occipital condyle	144	—
Width between the medial borders of the infratemporal fenestrae	124	—	Length of maxillary tooth row	155	207

Table II

Comparison of Characters in Crocodiles

P—primitive T—transitional A—advanced X—absent

Character	Archaeosuchia	Protosuchia	Mesosuchia	Eusuchia
Development of secondary palate	P	?	T	A
Position of postorbital bar	P	P	T	A
Orientation of the orbits	A	P	A	A
Orientation of the external nares	A	P	A	A
Dental differentiation	P	P	T	A
Relative length of the snout	A	P	A	A
Presence of palatal teeth	P	?	A	A
Sculptured cranial table	A	P	A	A
Skull height	A	P	A	A
Antorbital fenestra	T	A	T	A
Auditory canal	P	X	T	A
Vertebral structure	P	P	T	A
Rib articulations	P	T	A	A

Plate 1. Dorsal view of skull of *Proterochampsa barrionuevoi*, MCZ 3408. × ½ approx.

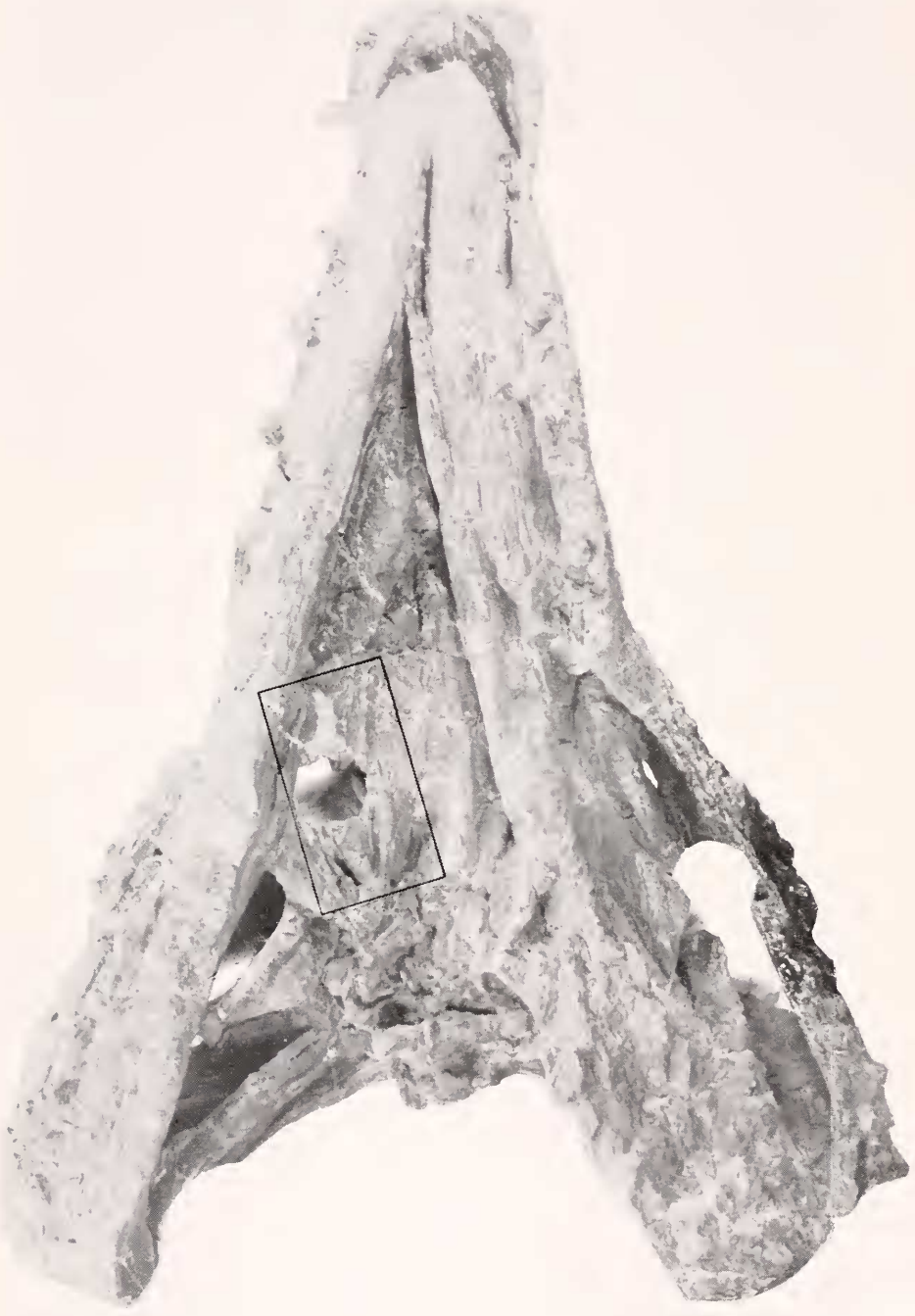


Plate II. Ventral view of skull of *Proterochompso barrionuevoi*, MCZ 3408, showing mandible crushed into skull. × ½ approx.

Plate III. Inset from Plate II; arrows show pterygoid teeth, MCZ 3408. × 2.

Plate IV. Ventral aspect of skull and mandible in stereoscopic view, MCZ 3408. × 1/3.

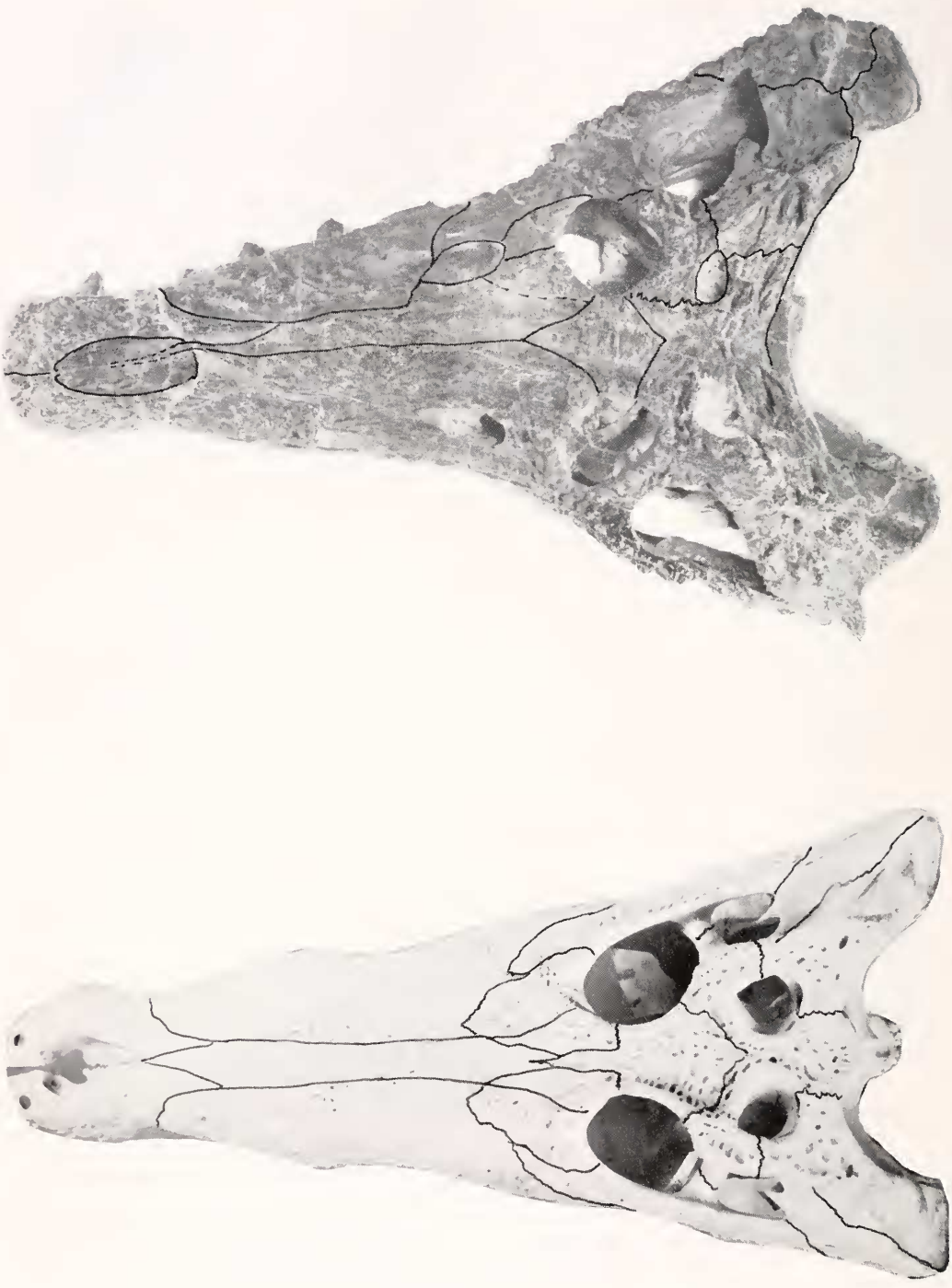


Plate V. Comparison of *Proterochampsa barrionuevoi*, MCZ 3408 (top), and *Crocodylus niloticus* (bottom), in dorsal view × 1/3.

Plate VI. Dorsal view of *Proterochampsa barrionuevoi*, MACN 18165, partially restored. × ½ approx.

Plate VII. Ventral view of *Proterochampsa barrionuevoi*, MACN 18165, showing secondary palate and internal nares.

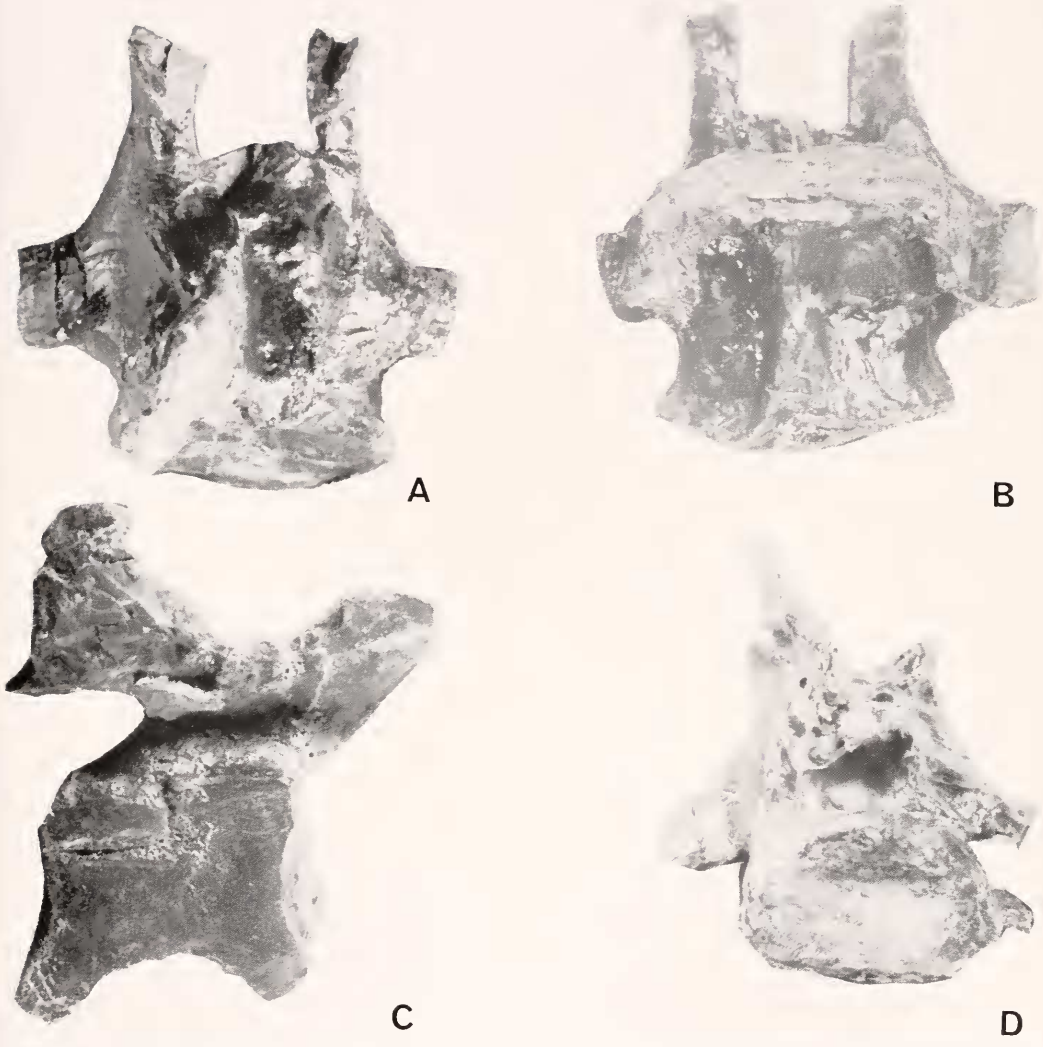
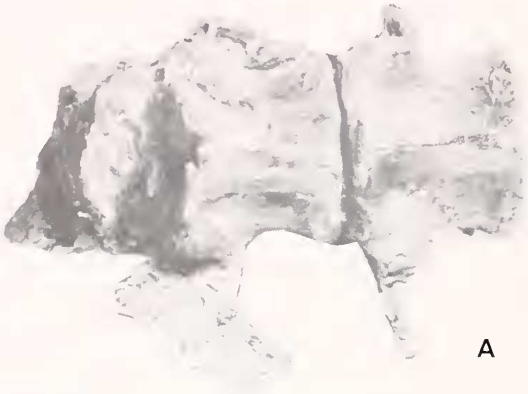
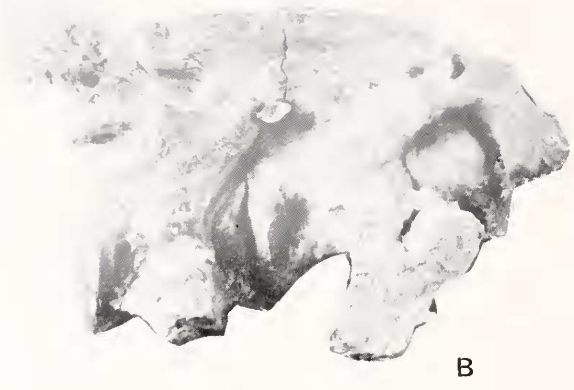


Plate VIII. A, B, D, Fourth cervical vertebra in dorsal, ventral, and anterior views, respectively. C, Longitudinal section of fifth cervical vertebra, MCZ 3408. × 2.





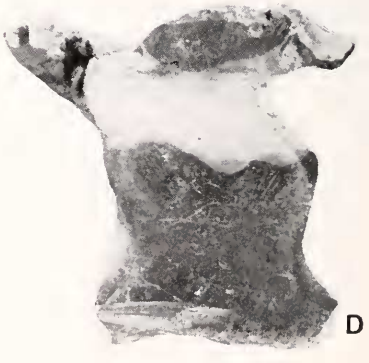


Plate IX. A, Atlas, axis, and third cervical in ventral view, anterior end to the left. B, Side view of atlas, axis, and third cervical, anterior end to the right. C, and D, Fifth cervical in side view and langitudinal section, MCZ 3408. × 2.